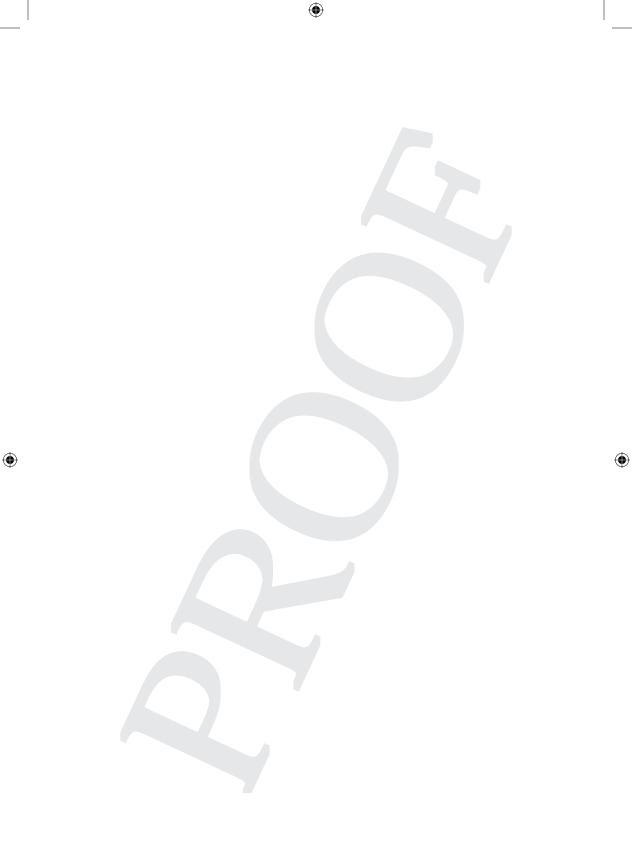
Part II Are All Concepts Learned?

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3 Beyond Origins

Developmental Pathways and the Dynamics of Brain Networks

Linda B. Smith, Lisa Byrge and Olaf Sporns

The invitation asked that we write on the question of whether concepts are innate or learned, with the idea being that we would take the side that they are learned. We cannot do the assigned task because the question, while common, is ill-posed. The terms *concept* and *innate* lack formal definitions. *Innate* has no standing within 21st century biological developmental processes (Stiles, 2008). *Learning*, in contrast, has many formally specified definitions (e.g., habituation, reinforcement learning, supervised learning, unsupervised learning, deep learning, and so forth; see Hinton, Osindero, & The, 2006; Michalski, Carbonell, & Mitchell, 2013) that have found many real-world applications in machine learning and have analogues in some forms of human learning. But surely the intended question was not whether the human mind is equivalent to implementations of machine-learning algorithms or in some way different. If so, our answer would be "different." Instead, we interpret the intended question to be about the *development* of the basic architecture of human cognition.

In brief, our answer to that question is this: Human cognition emerges from complex patterns of neural activity that, in fundamentally important ways, depend on an individual's developmental and experiential history (Byrge, Sporns, & Smith, 2014). Dynamic neural activity, in turn, unfolds within distributed structural and functional brain networks (Byrge et al., 2014). Theory and data implicate changing brain connectivity (i.e., changing brain networks) as *both* cause and consequence of the developmental changes evident in human cognition. These developmental changes emerge within a larger dynamic context, constituting a brain–body–environment network, and this larger network also changes across time. Understanding the development of human cognition thus requires an understanding of how brain networks together with dynamically interwoven processes that extend from the brain through the body into the world shape developmental pathways (Thelen & Smith, 1994; Chiel & Beer, 1997; Byrge et al., 2014).

In the chapter that follows, we attempt to flesh out this contemporary understanding of the "origins" of human cognition. We conclude that the traditional notions of "concepts" and "innateness" have no role to play in the study of the mind.

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Brain Networks

There are specialized brain regions that have been associated with specific cognitive competencies; however, research over the last 20 years has shown that different brain regions cooperate with one another to yield systematic patterns of co-activation in different cognitive tasks (Sporns, 2011). These patterns of cooperation depend on and reveal two kinds of brain networks: structural and functional networks. Structural networks are constituted by anatomical connections linking distinct cortical and subcortical brain regions. Functional networks are constituted by statistical dependencies among temporal patterns of neural activity that emerge in tasks but are also evident in task-free contexts (also called resting-state connectivity). For example, during reading, when left inferior occipitotemporal regions (linked with visual letter recognition) are active, temporally correlated evoked activity is also observed in left posterior superior temporal cortex (linked with comprehension) and in left inferior frontal gyrus (linked with pronunciation, see Dehaene et al., 2010). These regions thus form part of a "reading functional network" and jointly coordinate their activity during reading. Parts of this reading network are also involved in other functional networks, including spoken language production and on-line sentence processing (Dehaene et al., 2010; Monzalvo & Dehaene-Lambertz, 2013). This is the general pattern for all of human cognition; all of our various everyday activities recruit different assemblies of neural components, and so each individual component is involved in many different kinds of tasks.

Over time, brain networks change in some respects and remain stable in others. Structural networks are relatively stable, but they do change over the longer time scales of days, weeks, and years. Functional networks are much more variable, especially when observed on short time scales, but they also exhibit highly reproducible features over time, as can be seen in resting-state connectivity patterns. Changes in functional networks can therefore be measured over multiple time scales. At the time scale of milliseconds to seconds, functional networks undergo continual change, reflecting spontaneous and task-evoked fluctuations of neural activity (see Byrge et al., 2014 for a review). Over longer time intervals of several minutes, functional networks exhibit robustly stable features across and within individuals even at rest, features that are thought to reflect the brain's intrinsic functional architecture (Raichle, 2010). Nonetheless, these more stable features of functional networks also change over longer time scales, in response to the history of individuals (e.g., Tambini, Ketz & Davichi, 2010; Harmelech, Preminger, Wertman, & Malach, 2013; Mackey, Singley, & Bunge, 2013).

There are many examples of such long-term change. For example, perceptual learning changes the psychophysics of discrimination by changing the degree to which spontaneous activity between networks is correlated (e.g., Lewis et al., 2009). Likewise, mastering challenging motor tasks or musical training has been shown to lead to long-lasting changes in functional resting-state networks (Dayan & Cohen, 2011; Luo et al., 2012). Finally, when children learn to recognize and write letters, this leads to changes in the co-activation of motor and visual areas

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(James & Engelhardt, 2012). Importantly, these changes in functional networks do not just affect one task but have cascading consequences for many tasks. This is because stimulus-evoked activity is always a perturbation of ongoing activity. Therefore, experience-dependent changes in patterns of ongoing (resting-state) functional connectivity in the brain may have an effect on the potential response of the system to intrinsic and extrinsic inputs.

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Structural and functional networks also interact. On short time scales, structural and functional networks mutually shape and constrain one another within the brain. On long time scales, both generate and are modulated by patterns of behavior and learning. But, over the longer term, and as a consequence of their own activity in tasks, these networks change. For instance, moment-to-moment fluctuations in intrinsic functional connectivity predict moment-to-moment variations in performance on tasks such as ambiguous perceptual decisions and detection of stimuli at threshold (see Fox & Raichle, 2007; Sadaghiani, Poline, Kleinschmidt, & D'Esposito, 2015). Further, there have been many demonstrations of experience-induced changes in brain networks, and these studies reveal that individual differences in both structural and functional brain networks are associated with differences in cognitive and behavioral performance (see Deco, Tononi, Boly & Kringelbach, 2015). Our purpose in reviewing these findings is to show that understanding human cognition-its potential and its constraints-requires understanding the multi-scale dynamics of brain networks.

The dynamic properties of brain networks also clarify conceptual issues relevant to the "origins" of human cognition. First, the role of connectivity goes beyond channeling specific information between functionally specialized brain regions. In addition, connectivity generates complex system-wide dynamics that enable local regions to participate across a broad range of tasks. Second, the role of external inputs goes beyond the triggering or activating of specific subroutines of neural processing that are encapsulated in local regions. Inputs act as perturbations of ongoing activity whose widespread effects depend on how these inputs become integrated with the system's current dynamic state (Fontanini & Katz, 2008; Destexhe, 2011). Third, the role of connectivity and the role of experience go beyond enabling the performance of specific tasks. They also produce alterations in the spontaneous (resting-state) activity across these networks, and these alterations can influence the response of the system in novel tasks (Byrge et al., 2014). Fourth, the cumulative history of perturbations as recorded in changing patterns of connectivity-in-the-moment and over progressively longer time scalesdefines the system's changing capacity both to respond to input and to generate increasingly rich internal dynamics.

A long time ago, with no knowledge of the dynamics of the human brain, William James (1890/1950) had it fundamentally right when he wrote:

our brain changes, and ... like aurora borealis, its whole internal equilibrium shifts with every pulse of change. The precise nature of the shifting at a given moment is a product of many factors ... But just as one of them is certainly the influence of the outward objects on the sense-organs during the moment,

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so is another certainly the very special susceptibility in which the organ has been left at that moment by all it has gone through in the past.

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(James, 1950, p. 234)

Brain-Body-Environment

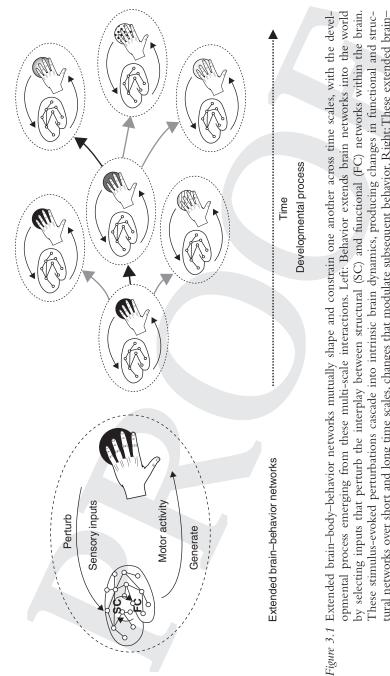
The changes in the brain—over the short term of momentary responses and over the longer term of developmental process—cannot be understood by studying the brain in isolation. Brain networks do not arise autonomously, but rather as the product of intrinsic and evoked dynamics, local and global neural processing, through constant interaction between brain, body and environment.

First, brain networks drive real-time behavior; this behavior in turn evokes neural activity that can change patterns of connectivity. For instance, when we hold a cup, write our name, or read a book, different but overlapping sets of neural regions become functionally connected and co-activation patterns emerge across participating components (Sporns, 2011). At multiple time scales, these co-activation patterns evoke changes within components and across the networks that extend beyond the moment of co-activation. This leads to further enduring functional and structural changes. Evoked neural activity from performing even relatively brief tasks such as looking at images causes perturbations to intrinsic activity that last from minutes to hours (e.g., Han et al., 2008; Northoff, Qin, & Nakao, 2010) and are functionally relevant, predicting later memory for the seen images (Tambini et al., 2010). These "reverberations" of evoked activity may also modulate structural topology via longer-lasting changes in synaptic plasticity and thus downstream activation patterns. Extensive practice in tasks such as juggling produces changes in the structure of cerebral white matter (Sampaio-Baptista et al., 2013) over slow time scales of weeks and longer (Zatorre, Fields, & Johansen-Berg, 2012) with task-induced modulations of functional and structural connectivity occurring in tandem (Taubert et al., 2011). All of this strongly suggests that an individual brain's network topology and dynamics at one time point reflect a cumulative history of its own past activity in generating behavior.

Second, behavior does not stop at the body but also physically affects and makes changes in the world (Clark, 1998). Behavior extends brain networks into the environment, coupling brain activity in real time to sensory inputs. Coordinated, distributed neural activity generates behavior. By its perceptible effects on the world—an object moved, a noise heard, a smile elicited—that behavior evokes coordinated neural activity across the brain. This real-time interaction of brain, behavior, and sensory inputs dynamically couples different regions in the neural system, modulates functional connectivity, and thereby drives change across functional and structural networks. We use Figure 3.1 to illustrate these ideas. When we hold and look at an object, brain networks drive the coordination of hand, head, and eye movements to the held object. As we interact with that object, through moving eyes, heads, and hands, we actively generate dynamic sensory-motor information that drives and perturbs neural activity and patterns of connectivity.

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behavior networks undergo profound changes over development, with changes in the dynamics of the body and behavior tural networks over short and long time scales, changes that modulate subsequent behavior. Right: These extended brain-(e.g. sitting, crawling, walking, or reading) creating different regularities in the input to the brain-and in turn modulating functional and structural networks of the brain, which in turn modify later behavioral patterns.

There is a remarkable amount of behavioral data from developmental psychology consistent with these claims (illustrated in Figure 3.1) about object manipulation, in particular. In human infants, recognition of the three-dimensional structure of object shape depends on and is built from the rotational information generated by the infant's own object manipulations (e.g., Pereira, James, Jones, & Smith, 2010; Soska, Adolph, & Johnson, 2010; James, Jones, Smith, & Swain, 2014). But the core developmental idea is older. Piaget (1952) described a pattern of infant activity that he called a secondary circular reaction. A rattle would be placed in a 4-month-old infant's hands. As the infant moved the rattle, it would both come into sight and make a noise. This would arouse and agitate the infant, causing more body motions, which would in turn cause the rattle to move into and out of sight and to make more noise. Infants at this age have very little organized control over hand and eye movement. They cannot yet reach for a rattle and, if given one, they do not necessarily shake it. But if the infant accidentally moves it, and sees and hears the consequences, the activity will capture the infant's attention-moving and shaking, looking and listening-and through this repeated action the infant will incrementally gain intentional control over the shaking of the rattle.

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Piaget thought this pattern of activity—an accidental action that leads to an interesting and arousing outcome and thus more activity and repeated experience of the outcome—to be foundational to development itself. Circular reactions are perception—action loops that create opportunities for learning. In the case of the rattle, the repeated activity teaches the infant how to control their body, which actions bring held objects into view, and how sights, sounds, and actions correspond. Piaget believed this pattern of activity, involving multimodal perception—action loops, to hold the key to understanding the origins of human cognition. The core idea of a cyclical reaction and its driving force on development is now understandable in the dynamics of brain networks. Holding and shaking the rattle couples different brain regions, creating a network, both in the generation of that behavior as well as in the dynamically linked sensory inputs created by its effects upon the world.

This is an example of the fundamental role played by a brain-body-environment network and it is the answer, just as Piaget saw, to the "origins" question (Sheya & Smith, 2010). Sampling of the external world through action creates structure in the input, which in turn perturbs ongoing brain activity, modulating future behavior and input statistics, and changing both structural and functional connectivity patterns. But this active sampling of the world is itself driven by neural activity, as motor neurons modulated by intrinsic neural activity and network topology guide the movements of eyes, heads, and hands. The brain's outputs influence its inputs, and these inputs in turn shape subsequent outputs, binding brain networks—through the body—to the environment over short time scales, and cumulatively over the course of development.

Developing Brain-Body-Behavior Networks

With development, changes are seen across all aspects of this cyclical process: the brain, its outputs, and its inputs. The development of brain networks is

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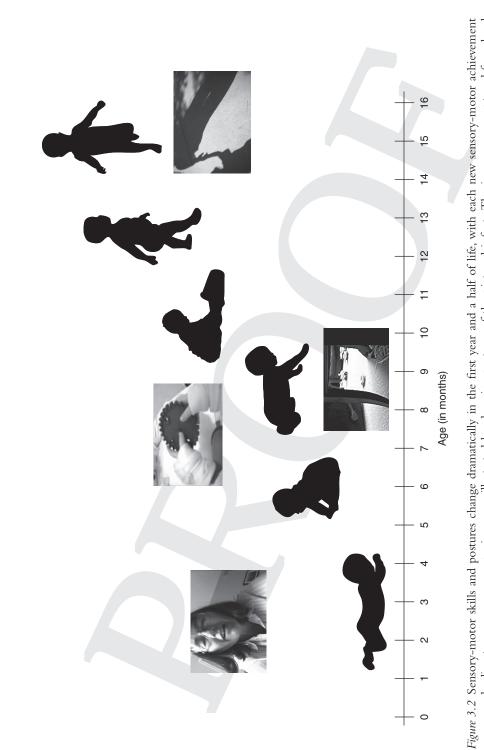
protracted, extending from postnatal pruning and myelination to synaptic tuning and remodeling over the lifespan (Stiles, 2008; Hagman, Grant, & Fair, 2012). In early human development, the body's morphology and behavior change concurrently, which results in continual but developmentally ordered changes in the input statistics. Figure 3.2 illustrates the dramatic changes in the motor abilities of humans over the first 18 months of life. A large literature documents dependencies between these specific motor achievements and changes in perception and other developments in typically (see Bertenthal & Campos, 1990; Smith, 2013; Adolph & Robinson, 2015) and atypically developing children (Bhat, Landa, & Galloway, 2011). For example, pre-crawlers, crawlers, and walkers have different experiences with objects, different visual spatial experiences, different social experiences, and different language experiences that are tied to posture and can be influenced by experimentally changing the infant's posture (Adolph et al, 2008; Smith, Yu, Yoshida, & Fausey, 2015,). Input statistics change profoundly with every change in motor development, and the constraints of the developing body on the brainbody-environment network may be essential to explaining why human cognition has the properties that it does.

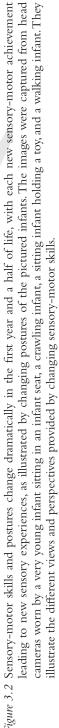
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Recent research in egocentric vision provides a strong case study. Egocentric vision is the first-person view, as illustrated in Figure 3.2. The first-person view has unique properties and is highly selective because it depends on the individual's momentary location, orientation in space, and posture (see Smith, Yu, Yoshida, & Fausey, 2015, for review). First, the scenes directly in front of infants are highly selective with respect to the visual information in the larger environment (e.g., Yu & Smith, 2012; Smith et al., 2015). Second, the properties of these scenes differ systematically from both adult-perspective scenes (e.g., Smith, Yu, & Pereira, 2011) and third-person perspective scenes (e.g., Yoshida & Smith, 2008; Aslin, 2009; Yurovsky, Smith, & Yu, 2013), and they are not easily predicted by adult intuitions (e.g., Franchak, Kretch, Soska, & Adolph, 2011; Yurovsky et al., 2013). Third, and most critically, the information and regularities in these scenes are different for children of different ages and developmental abilities (Kretch, Franchak, & Adolph, 2014; Jayaraman, Fausey, & Smith, 2015; Fausey, Jayaraman, & Smith, 2016).

Infant-perspective scenes change systematically with development because they depend on the perceiver's body morphology, typical postures and motor skills, abilities, interests, motivations, and caretaking needs. These all change dramatically over the first two years of life, and thus collectively serve as developmental gates to different kinds of visual data sets. In this way, sensory-motor development bundles visual experiences into separate data sets for infant learners. For example, people are persistently in the near vicinity of infants during their first two years and people have both faces and hands connected to the same body. But analyses of a large corpus (Fausey et al., 2016) of infant egocentric scenes captured in infant homes during everyday activities shows faces to be highly prevalent for infants younger than 3 months and much rarer for infants older than 18 months. In contrast, for younger infants, hands are rarely in view but, for older infants, hands acting on objects (either their own or others') are nearly continuously in view. Infants—through the rewarding dynamic cycles of face-to-face play—generate regularities in behavior and sensory inputs that are prior to and fundamentally

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different from the regularities generated by toddlers acting and observing the actions of others on objects.

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Brain networks change, bodies and what they do change, and the environment and its regularities change in deeply connected ways, with causes and consequences inseparable within the multi-scale dynamics of the brain-behavior-environment network. Theories of how evolution works through developmental processes have noted how evolutionarily important outcomes are often restricted by the density and ordering of different classes of sensory experiences (e.g., Gottlieb, 1991). This idea is often conceptualized in terms of "developmental niches" that provide different environments with different regularities (e.g., West & King, 1987; Gottlieb, 1991) at different points in time. These ordered niches—like a developmental period dense in face inputs or dense in hand inputs—play out in the development of individuals in real time and have their causes and consequences in the dynamic interplay of structural and functional brain networks through the body and in the world across shorter and longer time scales.

Primarily because of limitations in brain imaging technology, there is presently little direct evidence linking these changes in motor development and multisensory input to changes in brain networks in infants and toddlers. However, studies of older children learning to read, write, and compute provide direct evidence of brain networks being modulated by changes in behavior and input statistics (James, 2010; Hu et al., 2011; Li et al., 2013). Literacy acquired during childhood and adulthood is associated with largely similar patterns in structural (De Schotten et al., 2014) and functional (Dehaene et al., 2010) brain networks, underscoring the importance of behavior in creating those changes.

The dynamics of the brain-behavior-environment network-its adaptability, its core properties, and its development-have profound theoretical implications for understanding human cognition. Developmental changes in experiences and in the active sampling of information restructure the input statistics and over time yield changes in brain network topology and dynamics, which in turn support and influence behavior and new experiences. The sources of brain changes relevant to some development can be indirect and overlapping, with handwriting practice influencing reading networks (James, 2010), and reading practice influencing auditory language networks (Monzalvo & Dehaene-Lambertz, 2013). Many behavioral changes-learning to walk, manipulating objects, talking, joint action with others, learning to read-are common and linked with age, and thus seem likely to contribute to the age-related changes being reported in brain network structure and function (Johnson & De Haan, 2015; Pruett et al., 2015). In sum, the changing dynamics of the child's body and behavior modulate the statistics of sensory inputs as well as functional connectivity within the brain, which contribute to developmental changes in the functional and structural networks that constitute the human cognitive system.

Pathways Not Origins

Developmental theorists often refer to the "developmental cascade," and do so most often when talking about atypical developmental processes, such as how

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motor deficits and limits on children's ability to self-locomote cascade into the poor development of social skills (Adolph & Robinson, 2015) or how disrupted sleep patterns in toddlers start a pathway to poor self-regulation and conduct disorder (Bates et al., 2002). But the cascade is the human developmental process for cognition, typical and atypical alike, and it is the consequence of the historydependence of brain-body-environment networks. Like evolution and culture, new structures and functions emerge through the accumulation of many changes. As William James noted in the earlier quote, we are at each moment the product of all previous developments, and any new change-any new learning-begins with and must build on those previous developments. Because of this fact about development, we submit that the "origins" question (and all talk about nature and nurture) is hopelessly outmoded and must be replaced with the "pathways" question. Rather than ask whether human cognition is innate or learned, we should ask about the nature of the pathway leading to mature human cognition. In biology and embryology, a developmental pathway is defined as the route, or chain of events, through which a new structure or function forms. Thus embryologists delineate the pathways-the details of the chains of events-that lead to the new structures of a neural tube or a healthy liver.

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These pathways are evident in cognitive development as well. For example, object handling and manipulation by toddlers generates the sensory input critical to the typical development of three-dimensional shape processing (Pereira et al., 2010), stabilizes the body and head and supports sustained visual attention (Yu & Smith, 2012), makes objects visually large, centered and isolated in toddler visual fields, which support the learning of object names (Yu & Smith, 2012). By simultaneously indicating the direction of the toddler's momentary interests to others, object handling and manipulation invites social interactions and joint attention to an object with social partners (Yu & Smith, 2013). Joint attention to an object with a mature partner extends the duration of toddler attention and may train the self-regulation of attention (Yu & Smith, 2016). But holding and manipulating an object depends on stable sitting (Soska et al., 2010), and stable sitting depends on trunk control and balance (Bertenthal & von Hofsten, 1998). In this way, trunk control is part of the typical developmental pathway for object name learning and for the self-regulation of attention (Smith, 2013).

Just as in embryology, the pathways in behavioral development and the development of brain networks will be complex in three ways that challenge the oldfashioned questions about origins. First, change is multi-causal—that is, each change may be dependent on multiple contributing factors. Second, there may be multiple routes to the same functional end. Third, change occurs across multiple time scales that bring the more distant past into direct juxtaposition with any given current moment. Because developmental pathways may be complex in these ways, the question about necessary or sufficient causes, about "origin," becomes moot. Indeed, in the study of developmental pathways at the molecular level, researchers characterize prior states that set the context for the next event in the chain of developmental events as "permissive to." So, for example, in behavioral development we might say that trunk control is permissive to object manipulation and object manipulation is permissive to object name learning.

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What About Cognition?

Traditional views of cognition derive from a separation of mind from the corporeal. In this view, mental life may be partitioned into three mutually exclusive parts: sensations, thought, and action (e.g., Fodor, 1975). Cognition was strictly about the "thought" part and was understood to be amodal, propositional, and compositional, and thus to be fundamentally different from the processes responsible for perceiving and acting, which must deal in time and physics (Pylyshyn, 1980). Although this stance may be weakening given the juggernaut of advancing human neuroscience, many of the theoretical constructs in the study of human cognition and its development have their origins in the traditional view and thus these theoretical constructs are usually understood as strictly cognitive, and neither defined in terms of nor linked to the dynamics of brain, behavior, and world. Thus one might ask: What is the role of these constructs—knowledge, concepts, reference, aboutness, representation, and symbols—within the perspective offered here?

As a first step in his argument for a language of thought, Fodor (1975) made a cogent argument against reductionism. He noted that there could be lawful relations at one level of analysis and lawful relations at another that did not map coherently and systematically to each other, and that, to capture important generalizations, phenomena needed to be studied-and explained-at the proper level of analysis. This is surely correct (although understanding the bridges between levels is also where field-changing and barrier-breaking advances often occur). But can constructs such as concepts, innate, learned, and core knowledge be saved by this "level of analysis" move, which states that they are about phenomena at a different level of analysis than the dynamics of brain-behavior-environment networks? Although there are phenomena for which cognitive analyses might be appropriate, we would argue that development is not one of them. As Fodor clearly argued, phenomena need to be understood at the level of analysis that can reveal the explanatory principles for the phenomenon in question. Human cognitive development is a phenomenon of multi-scale, multi-causal change in a very complex system and thus the relevant theory about the development of human cognition must be in these terms.

The old-fashioned dichotomy of origins—learned versus innate—is ill-posed because of the history-dependence and multiple causality of developmental processes—from conception onward. The brain–behavior–environment network begins to form prior to birth when the developing brain begins generating behaviors that affect the fetal environment (e.g., Brumley & Robinson, 2010). The "origins" of every aspect of cognition in a present moment lie in how the individual's developmental pathway has carved out the structural properties and in-the-moment neural activity up to this moment in time.

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